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BATS OF THE ANTILLEAN ISLAND OF GRENADA: A NEW ZOOGEOGRAPHIC PERSPECTIVE

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The island of Grenada is the southernmost of the Lesser Antilles, lying 130 km north of Trinidad and 135 km north of the Venezuelan mainland. It measures 34 km north to south and 19 km east to west and has an area of 311 square km. Grenada and the Grenadines northward to Bequia stand on the large submarine Grenada Bank. At 183 m depth, the bank is 179 km long. The Grenadines cover the bank to its northern end, but the bank extends for 39 km south of Grenada with no islands. During the last Ice Age, Grenada and the Grenadines must have been one large island that extended from within 2 km of St. Vincent in the north to within 80 km of South America in the south.

Grenada is a volcanic island with many extinct craters, including the one occupied by Grand Étang Lake, located at 530 m and covering 14 ha. A central ridge of mountains runs like a north to south "spine" with Mount St. Catherine at 840 m the highest point. The island has an average annual temperature of 29°C. Rainfall varies from 75 cm annually in the Point Salines area on the southwestern coast to 150 cm in other coastal areas to 380 cm in the mountainous interior. The rainy season lasts from June to December, with November usually the wettest month. Grenada lies south of the primary hurricane belt and was last hit by a major hurricane in 1955, when Hurricane Janet hit the island with winds of up to 210 kph.

We have studied and collected bats on Grenada on 5 occasions—10-12 August 1967 (Phillips); 22-26 May 1980 (Baker and Genoways); 28 May to 2 June 1986 (Genoways and Phillips); 26 to 29 May 1987 (Genoways and Phillips), and 18-19 July 1989 (Phillips). Vegetation and sites that we visited are discussed in the species accounts below. Generally, there is great variety in the island's plant communities. Most of the original native forest was cleared during the plantation era so what is seen today is primarily secondary growth. The Grand Étang Reserve in the southern mountains covers 1520 ha and protects the forest and the island's watershed. Because the prevailing wind is from the east, the western side of the island is relatively arid in comparison to the eastern coastal zone and montane slopes. In the southwest and along the rocky west coast, vegetation is dominated by arid tropical and scrubland plants, including agave, prickly pear and other cacti, acacia, and calabash trees. Other areas, especially the east coast, have mangrove swamps, low wet areas used for tropical agriculture, and coconuts. The higher elevations have rainforest with trees, including mahogany, teak, saman, and blue mahoe, reaching up to 30 m to form a canopy. These areas include a variety of other native plant species such as bamboo, heliconia, balsa, mountain cabbage palm, and bird of paradise flower. Grenada is known as the Island of Spice and has numerous exotic cultivated spices and Neotropical fruit trees, including bananas, bay, breadfruit,

cocoa, guava, mango, nutmeg, papaya, passion fruit, pigeon peas, pimento, sugar apple, soursop, turmeric, and vanilla.

Based on our studies, the chiropteran fauna of Grenada consists of 12 species including representatives of the families Emballonuridae (1 species), Mormoopidae (1), Noctilionidae (1), Phyllostomidae (7), Vespertilionidae (1), and Molossidae (1). A thirteenth species, *Carollia perspicillata*, has been reported

from the island. In fact, it was the first species to be reported from Grenada (Dobson, 1878), but we find no evidence of a contemporary population of this bat on Grenada. We, thus, consider the one existing specimen to be an erroneous record or an accidental occurrence. G. M. Allen was the first scientist to make a systematic collection of bats from Grenada when he visited the island in August and September of 1910. His report of this collection (Allen, 1911) recorded the occurrence of six species on the island.

METHODS

Species accounts given below are arranged in systematic order and present data on systematics, habitats, distribution, and reproduction for each species. All linear measurements are given in millimeters and were taken with electronic calipers. Distances are recorded in kilometers (km) or miles (mi), depending upon the units from the original collector. Elevations and depths are in

meters (m), area in square kilometers (sq km) and hectares (ha), and rainfall in centimeters (cm). Statistical analyses were performed using the StatView® software package (Sager, 1992). The paired t-test gave standard statistics for each sample and statistical significance of differences in group means.

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of Nebraska State Museum (UNSM). Funding for our work came from a variety of sources and related projects, in particular NIH (RO1 to CJP and DEP), Hofstra University HCLAS grants (CJP), and Research Council, University of Nebraska-Lincoln (HHG). We would like to express gratitude to our field companions in doing this study, especially Dorothy E. Purno (DEP) and Scott C. Pedersen. Figure 1 was prepared by Angie Fox, Staff Artist, University of Nebraska State Museum.

SPECIES ACCOUNTS

Peropteryx macrotis phaea

G. M. Allen, 1911

Lesser Doglike Bat

Specimens examined (50).—ST. ANDREW: Mt. Pleasant Estate [near Adelphi], 24 (NMNH). ST. DAVID: Westerhall, 2 (NMNH). ST. GEORGE: Point Salines, 23 (MCZ). PARISH UNKNOWN: no specific locality, 1 (BMNH).

Remarks.—This species was not taken during our various surveys on Grenada; however, it was taken on several occasions by earlier investigators, which firmly

documents that the species has been a member of the chiropteran fauna of the island. Because the most recent date of capture for this species is 29 August 1910, it is tempting to think that the species no longer inhabits the island. The authors have spent extensive time surveying areas where the species was taken previously, but our work was almost exclusively done using mist nets. G. M. Allen (1911) made the following statement concerning the collecting of *Peropteryx* at Point Salines: "We found these bats in but one spot, a rather open cave on the seacliffs at Point Saline [= Point Salines], the extreme southern end of the island. They clung by both hind feet to the rough surfaces of the rocks, usually in

well-shaded, overhanging places; but, on being disturbed, would flit farther into the darker recesses of the cave. Others, however, flew about under a tree near the mouth of the cave, but eventually took shelter in adjoining fissures." A note on the specimens in the large collection of bats from Mt. Pleasant Estate stated "taken in rocks" and a note on the two specimens from Westerhall Estate stated "taken in hollow rock." We have not searched rock crevices and small caves on the island and this will be required before *P. macrotis* can be said to no longer occur on Grenada.

Although it is difficult to evaluate the gender ratio of bats in research collections (it is impossible to know the selective actions, if any, of the collector), it is interesting to notice that the ratio of females to males in our two largest samples were 12:12 at Mt. Pleasant Estate and 8:15 at Point Salines. G. M. Allen (1911) considered seven of the bats he collected at Point Salines on 29 August 1910 to not be adults. No other reproductive data were recorded for any of the specimens examined.

G. M. Allen (1911) described *P. m. phaea* based upon the material from Point Saline [= Point Salines]. He distinguished the Grenada populations from those on the South American mainland based primarily upon color, which was nearly uniform Prout's brown above and below as opposed to having a reddish cast. From the taxon *trinitatus* from Trinidad, *phaea* was distinguished by its longer length of forearm, being 42.5 (41-44.5) as opposed to 40.0 (39.0-41.0). Sanborn (1937) believed that the population on Grenada averaged smaller than mainland populations, but he was not able to characterize *trinitatus* with the material that he had at hand. Goodwin and Greenhall (1961) assigned specimens from Tobago to the mainland subspecies *P. m. macrotis*, while restricting the taxon *P. m. trinitatus* to Trinidad. They believed that the larger external and cranial size of the Tobago material supported this decision, with mean length of forearm of Tobago specimens (three females) being 46.5 (46.0-47.2) as opposed to 42.1 (41.0-43.0) for specimens from Trinidad (one male and three females), greatest length of skull 14.8 (14.7-15.0) versus 13.6 (13.2-13.9), and length of maxillary tooththrow 5.9 (5.8-6.0) versus 5.4 (5.3-5.5). Handley (1976) and Brosset and Charles-Dominique (1990) more recently have treated *P. macrotis* and *P. trinitatus* as distinct species. Handley

(1976) stated no reasons for this decision in Venezuela, but Brosset and Charles-Dominique (1990) working in French Guiana distinguished the two taxa based on the differing shape of the ears and tragus and the shorter skull (greatest length of skull: 14.0-15.2 versus 13.2, 13.2) with smaller teeth (length of maxillary tooththrow: 5.3-6.0 versus 4.7, 4.8) of *P. trinitatus*. Jones and Hood (1993) in a synopsis of South American emballonurids included both *trinitatus* and *phaea* as subspecies of *P. macrotis*, although this was done without comments on their reasons. Koopman (1994) uses the name *P. m. phaea* for the population on Grenada.

Comparing the measurements of our specimens from Grenada (Table 1) with those from other regions where similar data are available, it is clear that the Grenadan material most closely resembles the sample from Trinidad (Dalquest, 1951; Goodwin and Greenhall, 1961; Carter et al., 1981). Variation in the sample from Grenada encompasses the variation in the Trinidad sample for length of forearm, greatest length of skull, zygomatic breadth, and length of the maxillary tooththrow, whereas variation in the Trinidad samples encompasses the variation in the Grenada sample for breadth of postorbital constriction, which is the only other measurement available. The sample from Tobago is the most morphometrically distinct of those compared with the Grenadan sample. There is no overlap in the measurements of the these two samples in length of forearm, greatest length of skull, and length of the maxillary tooththrow. The sample from Grenada fills the gap in the range measurements between the two samples from French Guiana that are supposed to represent the species *Peropteryx macrotis* and *P. trinitatus*. In four measurements the sample from Grenada overlaps the lower end of the range of variation in the sample of *P. macrotis*, including length of forearm (overlap from 43.0 to 43.2), greatest length of skull (14.0 to 14.1), zygomatic breadth (7.9 to 8.2), and length of maxillary tooththrow (5.3 to 5.5). The two specimens of *P. trinitatus* from French Guiana fall at the lower end of the range of variation of the Grenada sample in length of forearm, greatest length of skull, and zygomatic breadth, whereas for breadth of the postorbital constriction the specimens from French Guiana are at the upper end of the range of variation and in length of maxillary tooththrow at 4.7 and 4.8, these are the two smallest specimens that have been considered in this study.

It is difficult to draw any meaningful taxonomic conclusions from these data. Morphologically, the sample from Grenada is clearly most similar to the material from Trinidad reported by Goodwin and Greenhall (1961), but this leaves the perplexing specimens from Tobago. It also is clear that to go beyond this point will require a comprehensive analysis of the *Peropteryx macrotis* complex in northeastern South America to determine if two species are present and, if there are two species, to thoroughly document their morphological differences. We would not be surprised to ultimately find that material from Grenada is best assigned to the same species and subspecies of *Peropteryx* as is found on Trinidad. The taxon *phaea* was poorly distinguished by G. M. Allen (1911), who based its distinctiveness primarily on pelage color, which is known to be polytypic.

It is worthy of note that *Peropteryx* is the only representative of the family Emballonuridae known to have reached the Antilles (Baker and Genoways, 1978). Although the family Emballonuridae is believed to be one of the oldest of extant chiropteran families, *Peropteryx* probably is a recent invader based upon its weakly defined morphological distinctiveness, reaching the island from the south from either Trinidad or the South American mainland. We believe that this invasion has occurred as over water dispersal. It is not understood why emballonurids are not more extensively distributed in the Antilles. Bats of similar size and habits, such as *Natalus* and *Myotis*, are widely distributed in the islands.

Pteronotus davyi davyi
Gray, 1838

Davy's Naked-backed Bat

Specimen examined (1).—PARISH UNKNOWN: no specific locality, 1 (BMNH).

Remarks.—The single specimen of Davy's naked-backed bat from Grenada was assigned to the nominate subspecies by Smith (1972). He also reported this species from the Antillean islands of Martinique, Dominica, and Marie Galante. Masson et al. (1990) have reaffirmed that *P. davyi* does occur as far north as Marie Galante; however, more recently Vaughan (1995) and Vaughan and Hill (1996) have reported the related species *Pteronotus parnellii* from St. Vincent, the first major island to the

north of Grenada. This was the first record of Parnell's mustached bat from the Lesser Antilles and indicates that this larger relative of Davy's naked-backed bat can be expected on Grenada. These species can be distinguished by the much larger size of *P. parnellii* and that the wing membranes of *P. davyi* fuse along the mid-dorsal line, whereas the wing membranes of *P. parnellii* attach lower on the sides so that the mid-dorsal area is covered by a band of hair. *P. d. davyi* was described based upon a specimen from Trinidad. The measurements of our single specimen (Table 1) fit within the range of measurements of samples from Trinidad and Dominica (Smith, 1972).

The specimen from Grenada was an adult male preserved in fluid. The skull has been removed from the individual allowing measurements to be taken. The specimen was obtained in 1894 from an unspecified location on Grenada by N. H. Smith (Jones, 1951).

Noctilio leporinus mastivus
(Vahl, 1797)

Greater Fishing Bat

Specimens examined (11).—ST. GEORGE: Chemin River, 1/2 km E Confer 12°01' N, 61°43' W, 6 (5 CM, 1 UNSM); 1/2 km E Vendôme, 12°05' N, 61°42.5' W, 1 (UNSM). PARISH UNKNOWN: E of Crawford, sea level (BMNH); no specific locality, 3 (2 NMNH, 1 MCZ).

Remarks.—Large fish-eating bats of the species *Noctilio leporinus* are common inhabitants of the islands of the Caribbean, and Grenada is no exception. These bats often are seen fishing over quiet bays and lagoons along the coast, and over pools and slow-moving areas of freshwater rivers. The species commonly roosts in small caves and hollow trees near these areas. Six of our specimens were taken in mist nets set over the Chemin River at a point that was no more than a kilometer from where it entered the sea. All were taken as they were hunting for small fish and invertebrates in the river. Most of the area adjacent to the river was open sugarcane fields, but several large trees on both sides of the river formed a canopy in some areas. The specimen from Vendôme was taken in another habitat type at an elevation of about 300 m. Nets were set over a small stream as it emerged from Grand Étang Forest Reserve. The

Table 1.—Length of forearm and cranial measurements of 12 species of bats from Grenada, West Indies. All measurements are in millimeters.

Sex/Cat. no. and Statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>PEROPTERYX MACROTIS PHAEA</i>								
Males								
N	6	6	6	6	6	6	6	6
Mean	42.6	13.7	12.3	8.0	2.6	7.1	5.3	6.0
SE	±0.32	±0.15	±0.15	±0.05	±0.03	±0.04	±0.05	±0.09
Minimum	41.3	13.2	11.8	7.8	2.5	6.9	5.1	5.6
Maximum	43.2	14.1	12.7	8.2	2.7	7.2	5.4	6.2
Females								
N	7	7	7	6	7	7	7	7
Mean	41.6	13.8	12.3	7.9	2.5	7.1	5.3	5.9
SE	±0.61	±0.09	±0.13	±0.12	±0.04	±0.05	±0.06	±0.11
Minimum	39.6	13.4	11.8	7.5	2.4	6.9	5.0	5.4
Maximum	43.1	14.1	12.7	8.2	2.6	7.2	5.5	6.3
<i>PTERONOTUS DAVYI DAVYI</i>								
Male								
94.9.7.1 BMNH	44.8	16.2	14.9	8.8	3.7	8.8	6.7	6.0
<i>NOCTILIO LEPORINUS MASTIVUS</i>								
Females								
N	4	5	5	5	5	5	5	5
Mean	84.9	26.4	23.6	18.4	6.7	16.6	10.1	12.1
SE	±1.30	±0.21	±0.26	±0.30	±0.11	±0.17	±0.04	±0.28
Minimum	82.0	25.8	22.8	17.4	6.5	16.2	10.0	11.1
Maximum	88.1	26.9	24.2	19.2	7.1	17.1	10.2	12.6

Table 1.— (continued.)

Sex/Cat. no. and Statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>GLOSSOPHAGA LONGIROSTRIS ROSTRATA</i>								
Males								
N	6	6	6	6	6	6	5	6
Mean	37.6	22.8	21.4	10.0	4.6	9.4	8.0	5.7
SE	±0.13	±0.11	±0.12	±0.10	±0.06	±0.08	±0.06	±0.07
Minimum	37.2	22.4	21.1	9.6	4.5	9.2	7.8	5.5
Maximum	38.1	23.2	21.8	10.2	4.8	9.7	8.1	5.9
Females								
N	6	6	6	6	6	6	5	5
Mean	37.9	23.1	21.5	9.8	4.7	9.4	8.0	5.9
SE	±0.43	±0.15	±0.16	±0.08	±0.06	±0.05	±0.14	±0.07
Minimum	36.0	22.7	20.9	9.5	4.6	9.3	7.7	5.7
Maximum	39.0	23.7	22.0	10.1	4.9	9.6	8.3	6.1
<i>ANOURA GEOFFROYI GEOFFROYI</i>								
Males								
N	10	10		10	10	10	10	10
Mean	42.0	25.0		11.0	5.0	10.5	9.4	6.2
SE	±0.22	±0.15		±0.07	±0.03	±0.05	±0.05	±0.06
Minimum	40.6	24.4		10.5	4.8	10.2	9.1	5.9
Maximum	43.2	25.6		11.2	5.1	10.8	9.5	6.5
Females								
N	10	10		10	10	10	8	10
Mean	42.9	25.2		10.9	5.0	10.4	9.5	6.2
SE	±0.28	±0.06		±0.07	±0.03	±0.08	±0.04	±0.05
Minimum	41.2	24.9		10.6	4.9	10.1	9.3	5.9
Maximum	44.3	25.5		11.3	5.2	10.9	9.6	6.4

Table 1.—(continued.)

Sex/Cat. no. and Statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>CAROLLIA PERSPICILLATA PERSPICILLATA</i>								
Female								
67.5.4.4 BMNH	41.8	22.9	19.9		5.4	10.8	7.2	7.3
<i>ARTIBEUS GLAUCUS BOGOTENSIS</i>								
Males								
63318 CM	39.3	20.3	18.4	11.5	5.0	10.5	6.5	8.5
63319 CM	40.6	21.4	19.1	11.7	5.0	10.8	6.7	8.7
151328 KU	40.0	21.2	18.6	11.8	5.2	10.6	6.8	8.8
19228 UNSM	38.0	20.7	18.7	11.9	5.1	10.6	6.8	8.7
Female								
14599 MCZ	39.8	21.0	18.8	11.7	5.0	10.9	6.7	8.7
<i>ARTIBEUS JAMAICENSIS GRENADENSIS</i>								
Males								
N	10	10	9	10	10	10	10	10
Mean	58.0	28.2	25.3	17.5	7.1	15.0	10.1	12.8
SE	±0.62	±0.19	±0.17	±0.14	±0.07	±0.11	±0.08	±0.11
Minimum	55.7	27.5	24.9	16.6	6.6	14.4	9.8	12.2
Maximum	61.8	29.4	26.0	18.0	7.3	15.5	10.6	13.3
Females								
N	32	32	32	32	32	32	32	32
Mean	58.1	28.2	25.0	17.2	6.9	15.0	10.0	12.6
SE	±0.27	±0.10	±0.09	±0.08	±0.03	±0.08	±0.05	±0.06
Minimum	55.7	26.8	23.8	16.5	6.7	13.7	9.4	11.8
Maximum	61.3	29.2	25.9	18.1	7.4	15.9	10.3	13.2

Table 1.— (continued.)

Sex/Cat. no. and Statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>ARTIBEUS LITURATUS PALMARUM</i>								
Males								
N	8	8	8	8	8	8	8	8
Mean	70.1	30.9	27.1	18.7	6.5	16.6	10.7	13.6
SE	±0.72	±0.23	±0.16	±0.17	±0.08	±0.13	±0.09	±0.12
Minimum	67.7	29.8	26.5	17.6	6.2	16.1	10.4	13.0
Maximum	72.4	31.5	27.8	19.0	6.7	17.2	11.2	14.1
Females								
N	7	7	7	7	7	7	7	7
Mean	72.0	30.8	27.0	18.5	6.5	16.4	10.7	13.4
SE	±0.81	±0.32	±0.28	±0.38	±0.09	±0.21	±0.12	±0.24
Minimum	69.0	29.5	25.9	16.9	6.2	15.3	10.2	12.7
Maximum	75.7	31.6	27.9	19.6	6.7	16.9	11.1	14.2
<i>STURNIRA LILIUM SEROTINUS</i>								
Males								
63412 CM	41.9	23.0	20.4	13.2	5.5	11.6	6.8	7.7
63413 CM	42.4	23.3	20.7	13.3	5.8	11.7	6.8	8.0
16493 UNSM	42.5	23.1	20.7	13.0	5.7	11.6	6.8	7.7
Females								
63414 CM	42.6	22.5	20.0	13.0	5.7	11.5	6.7	7.7
83426 CM	42.5	22.6	19.9	12.9	5.6	11.2	6.6	7.7
16494 UNSM	40.1	21.8	19.2	12.8	5.6	11.1	6.7	7.8

Table 1.—(continued.)

Sex/Cat. no. and Statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>MYOTIS NIGRICANS NIGRICANS</i>								
Males								
83427 CM	33.4	13.5	12.4	8.3	3.4	6.8	4.9	5.2
252600 NMNH	32.8	12.8	12.1	8.2	3.5	6.7	4.7	5.1
<i>MOLOSSUS MOLOSSUS MOLOSSUS</i>								
Males								
63415 CM	39.5	17.5	15.3	10.8	3.6	10.0	6.1	7.8
63423 CM	38.7	16.7	14.6	10.5	3.7	10.0	5.8	7.6
63424 CM	39.0	16.8	14.9	10.6	3.6	10.0	5.8	7.4
Females								
63421 CM	37.4	16.0	14.0	10.0	3.4	9.5	5.5	7.0
63422 CM	37.5	16.1	14.2	10.0	3.6	9.5	5.7	7.3
63428 CM	38.2	16.2	14.2	10.0	3.5	9.3	5.7	7.2

stream was one of the small upper tributaries of the Beauséjour River, which enters the Caribbean Sea approximately 5 km to the west-northwest. Habitat at this site was characterized by wet, dense montane forest, which became fairly open under the canopy away from disturbed areas. To the south of the edge of the Grand Étang Forest Reserve, much of the native vegetation was cleared for cocoa, bananas, mangos, and small garden plots, which were situated behind several homes that faced the nearby road. The stream was about 4 m wide and 30 cm deep. It ran fairly straight with a high canopy for nearly 50 m before dropping about 8 m over a concrete spillway.

Five females that were captured along the Chemin River were lactating on 23 May 1980 (4) and 28 May 1987. A sixth female from this location evinced no reproductive activity on 23 May 1980. No reproductive data were recorded for three male specimens that we examined (BMNH, MCZ, NMNH).

We have followed Davis (1973) in assigning our specimens to the subspecies *N. l. mastivus*, with a type locality of St. Croix, U. S. Virgin Islands. Specimens from throughout the Caribbean islands, Mexico, Central America, and northern South America were placed by Davis (1973) into this subspecies. The five females in our sample (Table 1) average slightly smaller in the five measurements reported by Davis (1973) than a sample from Trinidad and a pooled sample from throughout the West Indies. These average differences never exceed 0.6 mm and we believe are not of taxonomic significance.

Micronycteris megalotis
(Gray, 1842)

Brazilian Large-eared Bat

Specimen examined (1).— PARISH UNKNOWN: no specific locality, 1 (NMNH).

Remarks.— Because the Brazilian large-eared bat is represented from Grenada by a single, long-preserved museum specimen, we have questioned, as did Koopman (1958), whether it represented an existing population or a single accidental record. However, with report of a population of this species on St. Vincent by Vaughan (1995) and Vaughan and Hill (1997), it seems possible

that our specimen could represent a Grenadan population. Vaughan (1995) and Vaughan and Hill (1996) found *M. megalotis* roosting in coastal caves and feeding under rain forest canopy and along side of banana plantations near the rain forest. We netted many nights on Grenada in areas similar to where this species was found feeding on St. Vincent without taking any specimens of this species, so if *M. megalotis* presently occurs on Grenada, it must be in relatively low numbers.

Many recent authors (Handley, 1976; Brosset and Charles-Dominique, 1990; Simmons, 1996) have treated *M. megalotis* and *M. microtis* as separate species in contrast to the arrangement of Sanborn (1949) and Koopman (1993, 1994) where *microtis* was placed as a subspecies of *megalotis*. We are following the arrangement of recognizing two species with the limited material at hand, which results in *M. megalotis* being considered a monotypic species.

The specimen of *M. megalotis* in the National Museum of Natural History is an adult female with a length of forearm of 34.2. The specimen is stored in alcohol and the skull has not been extracted for study. The specimen has large ears characteristic of this species, but the membranes and pelage are so faded that no color determination is possible. The specimen does display the band between ears characteristic of the subgenus *Micronycteris* and, as Sanborn (1949) described it, the band is relatively low at the base of the ears rising to a triangle at the center. The relatively small notch in the band is located at the apex of the triangle.

Glossophaga longirostris rostrata
Miller, 1913

Miller's Long-tongued Bat

Specimens examined (231).— ST. ANDREW: Birch Grove, 19 (UNSM); Grand Étang, 4 (MCZ); Grenville, 5 (NMNH); Grenville Vale [near Granton], 6 (5 AMNH, 1 NMNH); 0.4 km S, 0.4 km W St. Margaret, 1600 ft, 12°06' N, 61°41.5' W, 3 (CM). ST. DAVID: 1 1/4 km S, 3/4 km W Beaton, 12°01.5' N, 61°42' W, 2 (CM); Westerhall Estate 13 (NMNH). ST. GEORGE: Chemin River, 1/2 km E Confer, 12°01' N, 61°43' W, 30 (22 CM, 8 UNSM); Fort Frederick, 2 (KU); French Ammunition Tunnels, 6 (KU); Point Salines, 3 (AMNH);

3 mi N, 1/2 mi E St. George's, 4 (KU); 1/2 mi NE St. George's, 2 (1 KU, 1 TTU); St. George's, 9 (MCZ); St. Paul's, 12°04' N, 61°44' W, 15 (11 CM, 4 TTU); Salt Pond, 1 (KU); True Blue 4 (3 AMNH, 1 NMNH); 1/2 km E Vendôme, 12° 05' N, 61°42.5' W, 53 (32 CM, 15 UNSM, 6 TTU); 1/2 mi E Vendôme, 1000 ft, 9 (KU). ST. JOHN: 3/4 km S, 1/2 km W Concord, 12°05.5' N, 61°44.5' W, 13 (11 CM, 2 TTU). PARISH UNKNOWN: no specific locality, 28 (NMNH).

Remarks.—Miller's long-tongued bat was one of the two most common and widespread species taken during our surveys on Grenada. It is known from the driest areas of the island around Point Salines and True Blue to the wettest areas that we visited at Vendôme and Birch Grove. The rain forest at the site we visited near Vendôme was relatively undistributed, but at Beaton and Chemin River the original vegetation is highly disturbed by agricultural activities. The sample of Miller's long-tongued bats from near Concord were netted in a banana plantation with a few of the old tall forest trees providing the overstory. Specimens from near Concord, as well as many others that we captured, had pollen covering their heads and shoulders. The yellow, powdery pollen was clearly visible in our lights at night.

Allen (1911) commented on the capture of the specimens from St. George's and Grand Étang that are housed in the Museum of Comparative Zoology. Specimens from St. George's were obtained "from holes, in the old fort on Richmond Hill." At Grand Étang (1800 ft = 545 m) specimens were observed "hanging to the ridge pole in a room of a disused stable, whence they obtained egress by means of a partially open window." The specimens from Westerhall Estate were "taken in hollow tree" in 1900 by Peter Gellineau (Miller, 1913a; Handley and Webster, 1987).

Females containing embryos, with crown-rump length of embryos indicated, were taken on the following dates (number of females from date with data in parentheses): 26 May, 5, 5, 7 (total of 6 adult females preserved); 27 May, 6 (2); 28 May, 5, 5 (2); 29 May, 5, 5 (4); 2 June, 9 (1); 18 July, no c-r (1); 19 July, no c-r for 2 (2). Females evincing no reproductive activity were taken on the following additional dates: 23 May (6 ex-

amined); 24 May (3); 30 May (3); 16 August (2); 17 August (1). A female netted on 24 May at St. Paul's was lactating and carried a non-volant juvenile male (length of forearm, 26.7), whereas females taken on 26 May and 17 August were lactating, but did not carry young. Volant subadult (as indicated by unfused wing phalangeal epiphyses) individuals were taken on the following dates: 24 May (2 males and 1 female, length of forearm, 37.2, 38.4, 38.0); 25 May (female, 35.6); 26 May (1 female and 2 males, 38.8, 36.7, 36.9); 28 May (female, 38.8). In a sample of 27 individuals preserved by A. M. Greenhall between 11 and 13 August 1955, 13 individuals were adults while 14 were subadults. The following testes lengths were recorded from adult males: 25 May, 5, 7; 26 May, 2, 4, 4, 5, 5, 5, 5; 27 May, 2, 3.5, 3.5, 4, 4, 4.5; 28 May, 3, 4, 4; 29 May, 2; 16 August, 2.5, 3, 5; 17 August, 4, 4. Although this species appears to breed during the rainy season, there are still not enough data available to describe the annual reproductive cycle (Wilson, 1979). Our reproductive data do agree with those published previously for this species from Trinidad (Goodwin, 1958; Goodwin and Greenhall, 1961) and Margarita Island, Venezuela (Smith and Genoways, 1974).

Table 1 gives the length of forearm and eight cranial measurements for samples of six males and six females from Grenada. Using a t-test, we found no evidence of significant secondary sexual variation between these samples.

The taxon *rostrata* originally was described by Miller (1913a) as a distinct species based on material from Westerhall Estate on Grenada, but quickly was moved by Miller (1913c) to a subspecies of *longirostris*. This taxonomic arrangement was maintained by the most recent reviewers of the species (Webster and Handley, 1986). *Glossophaga l. rostrata* was distinguished by Webster and Handley (1986) from other subspecies by its narrow rostrum and reduced postorbital swellings. The subspecies *rostrata* currently is known to occur on Grenada, Trinidad, Tobago, Grenadines, and St. Vincent. Two specimens previously reported by Miller (1913a, 1913c) from Dominica were shown by Handley and Webster (1987) to be mislabeled individuals from the original type series from Grenada.

Anoura geoffroyi geoffroyi

Gray, 1838

Geoffroy's Tailless Bat

Specimens examined (120).— ST. ANDREW: Birch Grove, 27 (UNSM); 0.4 km S, 0.4 km W St. Margaret, 1600 ft, 12°06' N, 61°41.5' W, 8 (CM). ST. GEORGE: 3 mi N, 1/2 mi E St. George's, 2 (KU); 1/2 km NE St. George's, 3 (KU); St. Paul's, 12°04' N, 61°44' W, 14 (CM); 1/2 km E Vendôme, 12°05' N, 61°42.5' W, 39 (34 CM, 5 UNSM); 1/2 mi E Vendôme, 1000 ft, 27 (KU).

Remarks.— Geoffroy's tailless bat first was reported from Grenada by Jones and Phillips (1970) based on the specimens listed above from the University of Kansas. Our work has shown that this species is more widespread on the island than the original records indicated with Geoffroy's tailless bat occurring in the more mesic areas on the island at locations that are above 250 m. This elevational limitation was shown in our work when *Anoura* was captured at the location 3 mi north and 1/2 mi east of St. George's at an elevation that is about 250 to 300 m, whereas less than 3 km to the north of this point at our location just south of Concord at about 60 m no specimens of this species were taken, but the related species, *Glossophaga longirostris*, was extremely abundant. We worked several sites along the southern and eastern coast and feel confident that Geoffroy's tailless bat does not occur in these low, dry areas dominated by thorn scrub, cacti, and agricultural fields. Goodwin and Greenhall (1961) believed that this species strictly roosted in caves on Trinidad. We can not confirm this observation on Grenada because all of our specimens were netted away from caves as they fed, particularly near planted orchards and banana plantations. We took the series of 14 individuals at St. Paul's in just such a situation on the evening of 24 May 1980. We placed our nets in the open grassy areas that had been cleared of native plants for fruit trees, which included bananas, mangos, papaya, guava, and nutmeg. There was little native vegetation left within several hundred meters of the area being netted, but a number of homes were scattered among the orchard and along the nearby road. Only *Anoura* and *Artibeus jamaicensis* and *A. lituratus* were taken during the evening.

All of our specimens were adults. None of the females taken on the following dates evinced any reproductive activity: 24 May (7 females); 25 May (3); 26 May (9); 27 May (1); 30 May (4); 1 June (2); 19 July (10); 16 August (2); 17 August (8). These observations would be in line with those made by Goodwin and Greenhall (1961) on Trinidad where they found gravid females with fetuses in advanced stages of development on 20 November, but fetuses were not found in females taken on 12 June or 17 October. Wilson (1979) commented on the rather unusual discrete late rainy season breeding period of *Anoura geoffroyi*. The following testes length were recorded for this species on Grenada: 25 May, 6, 6, 7; 26 May, 2, 5, 8; 30 May 6, 7; 1 June, 7; 16 August, 6; 17 August, 6, 6, 6, 7, 7, 7, 7, 7, 8.

Selected samples of males and females from Grenada were tested for secondary sexual variation using t-tests (see Table 1). No secondary sexual variation was found in six cranial measurements, but the length of forearm of females was significantly ($P < .05$) longer than that of the males.

Jones and Phillips (1970) made the following statement concerning the systematic relationships of this newly discovered population to the known population on Trinidad: "Preliminary study indicates that Grenadan *Anoura* average slightly larger than specimens from Trinidad and have a somewhat more inflated braincase, but they do not differ otherwise and probably represent the same subspecies (*A. g. geoffroyi* Gray)." Jones (1989) later confirmed this preliminary subspecific determination (see also Koopman, 1994). We tested a sample (8 males, 2 females in collections of Museum of Texas Tech University) from Trinidad against our combined sample from Grenada (Table 1) using t-tests to determine if any significant geographic variation was present. None of the seven measurement tested revealed any significant geographic variation between these two island populations. We, therefore, follow the earlier authors in assigning the Grenadan population to same subspecies as on Trinidad, which is currently considered to be *Anoura geoffroyi geoffroyi*.

Carollia perspicillata perspicillata
(Linnaeus, 1758)

Seba's Short-tailed Bat

Specimen examined (1).—PARISH UNKNOWN: no specific locality, 1 (BMNH).

Remarks.—*Carollia perspicillata* is represented from Grenada by a single specimen of an adult female deposited in the British Museum (Natural History). Based upon the catalogue number of the specimen (67.5.4.4), it would appear to have been registered into the collection in 1867. This specimen first was reported by Dobson (1878) under the name *Carollia brevicauda*. He indicated that the specimen had been acquired through purchase. Subsequent authors (Allen, 1911; Pine, 1972) have assigned this specimen to the species *C. perspicillata* and we agree with this assignment. Examining the characters used by Pine (1972) to distinguish species within the genus, this specimen possesses the following characteristics in agreement with *C. perspicillata*: size relatively large (see Table 1); the lower outer incisors, when viewed from above, obscured by canines; maxillary toothrow straight, not bowed or with a step; short hair covering the forearm; hair on mid-back about 6 mm.

Koopman (1989) omitted *Carollia* from his analysis of the bats from the Antilles and Jones (1989) considered the status of *Carollia* on Grenada as questionable. We here consider that the specimen from Grenada represents either an erroneous record or an accidental occurrence on Grenada. With a very old record based upon a purchased specimen, we feel that it is very likely that the locality data for this specimen are incorrect, but because we can not absolutely rule out this being an accidental record from Grenada, we have retained the species in this compilation of bats from the island. It is actually of some considerable interest that *Carollia perspicillata* is not found in the Antilles. The species is abundant and widespread on Trinidad, Tobago, and Little Tobago (Goodwin and Greenhall, 1961). Seba's short-tailed bat would appear to be successful in habitats disturbed by human or weather activities; therefore, the appropriate habitats would appear to be available on Grenada.

Artibeus glaucus bogotensis
Andersen, 1906

Lesser Gray Fruit-eating Bat

Specimens examined (5).—ST. ANDREW: Grand Étang, 1 (MCZ). ST. GEORGE: 8 mi N St. George's, 1 (KU); 1/2 km E Vendôme, 12°05' N, 61°42.5' W, 3 (2 CM, 1 UNSM).

Remarks.—The lesser gray fruit-eating bat has been reported previously from Grenada based upon a single specimen from Grand Étang (Koopman, 1958). This female bat was captured in November 1912. The species was not taken on the island again until 2 May 1980 when we netted two males (length of testes, 2, 5) at the edge of the Grand Étang Forest Reserve. Subsequently, we captured another male (length of testes, 4) on 19 July 1989 at the exact place where the specimens were captured in 1980. Therefore, all captures of this exceedingly rare species on Grenada have come from undisturbed montane forests at elevations above 1000 feet [=300 m]. We hypothesize that the continued existence of this species on Grenada is dependent upon the continued existence and health of these montane forests.

Koopman (1958, 1994) and subsequent authors have reported this species under the name *Artibeus cinereus*. Owen (1987) resurrected the generic name *Dermanura* for most of the smaller representatives of the genus *Artibeus* and treated this species as *Dermanura cinerea*. We have not followed his arrangement preferring instead to follow Koopman (1993, 1994), Lim (1993), Lim and Wilson (1993), Van Den Bussche et al. (1993, 1998), and Purno et al. (1996) in retaining the generic name *Artibeus* for these bats. Handley (1987) in describing a new species from Venezuela rearranged the small *Artibeus* into 10 species and six species groups. He restricted *Artibeus cinereus* to the Guiana region, coastal Brazil, and lower Amazon Basin and applied the name *Artibeus glaucus* to the northern South American form. The name *Artibeus glaucus bogotensis* appears to be the most appropriate trinomial to apply to populations on Trinidad and Tobago formerly designated as *Artibeus cinereus cinereus* (Handley, 1987; Koopman, 1993), although Koopman (1994) has used *A. cinereus bogotensis*.

Because the most obvious route of invasion of this species into the Antilles was from the south (Koopman, 1968; Jones and Phillips, 1970; Jones, 1989), we have compared our specimens with a sample from Trinidad (five males and five females from Las Cuevas in The Museum of Texas Tech University) to determine their subspecific status. Measurements of the four specimens from Grenada are presented in Table 1. Because the sample from Grenada was too small to test for secondary sexual variation, the Trinidad sample was tested to determine if the sexes could be combined for an analysis of geographic variation. None of the eight measurements tested revealed any significant (using t-test) secondary sexual variation so the sexes were combined in the next analysis. We compared the measurements of the four specimens from Grenada with the sample of 10 specimens from Trinidad using a t-test. The only significant ($P < 0.5$) difference was for zygomatic breadth—the sample from Grenada averaged 11.7, whereas the Trinidad sample averaged 12.3. Means for the two samples (Grenada followed by Trinidad) for the remaining seven measurements were as follows: length of forearm, 39.4, 40.6; greatest length of skull, 20.9, 20.8; condylobasal length, 18.8, 18.7; postorbital constriction, 5.0, 5.0; mastoid breadth, 10.7, 10.7; length of maxillary tooththrow, 6.7, 6.7; breadth across upper molars, 8.7, 8.8. Clearly, the specimens from Grenada are morphologically close to those from Trinidad and should be assigned to the same subspecies, which currently is believed to be *bogotensis*. All three specimens that we captured during our work also exhibited the dental character of only two rather than three lower molars that Handley (1987) believed was typical of *A. g. bogotensis*.

Artibeus jamaicensis grenadensis

Andersen, 1906

Jamaican Fruit-eating Bat

Specimens examined (330).— ST. ANDREW: Birch Grove, 20 (UNSM); 0.4 km S, 0.4 km W St. Margaret, 1600 ft, 12°06' N, 61°41.5' W, 2 (CM). ST. DAVID: 1 1/4 km S, 3/4 km W Beaton, 12°01.5' N, 61°42' W, 11 (CM); Westerhall Estate, 18 (NMNH). ST. GEORGE: Chemin River, 1/2 km E Confer, 12°01' N, 61°43' W, 45 (25 CM, 20 UNSM); Fort Frederick, 8 (KU); Grenville Vale [near Grafton], 1 (NMNH); 8 mi NE St. George's, 1 (KU); 3 mi N, 1/2 mi E St. George's, 9 (KU); 1/2 mi NE St. George's, 9 (KU); St. George's,

46 (MCZ); St. Paul's, 12°04' N, 61°44' W, 14 (12 CM, 2 TTU); 1/2 mi E Vendôme, 1000 ft, 8 (KU); 1/2 km E Vendôme, 12°05' N, 61°44.5' W, 76 (38 CM, 36 UNSM, 2 TTU). ST. JOHN: 3/4 km S, 1/2 km W Concord, 12°05.5' N, 61°44.5' W, 11 (9 CM, 2 TTU). PARISH UNKNOWN: no specific locality, 51 (48 NMNH, 2 MCZ, 1 BMNH).

Additional record.— Douglaston (Jones, 1951).

Remarks.— The Jamaican fruit bat, along with Miller's long-tongued bat, are the two most common and widespread species of bat on Grenada. It occurs in all habitats and at all elevations with the possible exception of the driest areas in the southwestern corner of the island around Point Salines. Allen (1911) reported a breeding colony of Jamaican fruit bats found in the recesses of the old fort on Richmond Hill in St. George's. Of the 30 adults in his sample, 26 were females. At Douglaston a large colony was found in the roof of a distillery (Jones, 1951).

At least since the work of Hershkovitz (1949), the subspecies *A. j. grenadensis* Andersen has been considered by most authors to be a junior synonym of *A. j. trinitatis* with a type locality on Trinidad. However, we believe that we have developed both morphological and genetic data that support the recognition of population on Grenada as a distinct subspecies to which the name *A. j. grenadensis* would apply. Table 2 presents the results of t-tests comparing samples of *A. j. trinitatis* from Trinidad and *A. j. schwartzi* from St. Vincent with the population on Grenada. The sample of *grenadensis* is significantly smaller than *schwartzi* in length of forearm and the seven cranial measurements at the $P < 0.001$ level. In fact the range of measurements of the two taxa only overlap in three measurements—breadth of postorbital constriction, mastoid breadth, length of maxillary tooththrow. The sample of *grenadensis* averaged significantly larger at the $P < 0.001$ level than the sample of *trinitatis* for length of forearm, greatest length of skull, condylobasal length, and zygomatic breadth and at the $P < 0.05$ level for breadth of postorbital constriction and breadth across upper molars. Means of the two samples were not significantly different for mastoid breadth and length of maxillary tooththrow. Therefore, *A. j. grenadensis* is morphologically distinct from the geographically nearest taxa, although it would appear to be slightly closer to *trinitatis* morphologically.

Table 2.—Morphometric comparisons of one external and seven cranial measurements of populations of *Artibeus jamaicensis* from Grenada, St. Vincent, and Trinidad. ns = not significant; * = $P < 0.05$; *** = $P < 0.001$.

Measurements and Statistics	Trinidad	Significance	Grenada	Significance	St Vincent
Length of forearm					
Number	16		42		8
Mean	55.8	***	58.1	***	63.6
Range	53.6-57.9		55.6-61.8		62.1-64.6
SE	±0.30		±0.25		±0.29
Greatest length of skull					
Number	16		42		8
Mean	27.6	***	28.2	***	30.9
Range	26.8-28.7		26.8-29.4		30.1-31.8
SE	±0.14		±0.09		±0.21
Condylobasal length					
Number	16		41		8
Mean	24.5	***	25.1	***	27.2
Range	23.7-25.1		23.8-26.0		26.5-28.0
SE	±0.11		±0.09		±0.24
Zygomatic breadth					
Number	15		42		8
Mean	16.8	***	17.3	***	19.3
Range	16.3-17.3		15.8-18.0		18.6-20.1
SE	±0.08		±0.07		±0.22
Breadth of postorbital constriction					
Number	16		42		8
Mean	6.9	*	7.0	***	7.4
Range	6.7-7.1		6.6-7.4		6.9-7.6
SE	±0.05		±0.03		±0.08
Mastoid breadth					
Number	16		42		8
Mean	15.1	ns	15.0	***	16.3
Range	14.5-16.4		13.7-15.9		15.7-16.7
SE	±0.12		±0.07		±0.13
Length of maxillary tooththrow					
Number	16		42		8
Mean	10.0	ns	10.0	***	10.8
Range	9.3-10.6		9.5-10.4		10.4-11.4
SE	±0.06		±0.04		±0.12
Breadth across upper molars					
Number	16		42		8
Mean	12.4	*	12.7	***	14.1
Range	11.6-13.3		11.8-13.2		13.5-14.7
SE	±0.09		±0.05		±0.16

Artibeus jamaicensis is the only Grenadan bat species for which we have genetic data. These data are in the form of mitochondrial DNA (mtDNA) haplotypes based on restriction endonuclease analyses (Phillips et al., 1989). Two aspects of the mtDNA data are highly relevant to our understanding of subspeciation as discussed in the previous paragraph, and to our overall understanding of the zoogeographic position of Grenada and its bat populations. First, in terms of mtDNA, *A. jamaicensis grenadensis* previously was reported to be genetically diversified in comparison to other island populations examined (Phillips et al., 1989). We recently reanalyzed the restriction site data by means of Arlequin genetic analysis software (ver. 1.0, Schneider et al., 1996) and expanded the survey to include bats from additional islands and Yucatan. We obtained the following estimates of nucleotide diversity in mtDNA in Antillean island populations of *A. jamaicensis*: Grenada, 0.0331; St. Lucia, 0.01226; St. Vincent, 0.00984; Barbados, 0.00795; Puerto Rico, 0.00326; Jamaica, 0.00174; Anguilla, 0; Bequia, 0. Nucleotide diversity obviously is independent of island size, and in general there is a decrease from south to north. The high nucleotide diversity of mtDNA in *A. j. grenadensis* in part reflects the fact that all of the haplotype lineages (labeled G, SV, and J) discovered in the Caribbean are represented on the island (Phillips et al., 1989, 1991). Another component of the diversity is a haplotype lineage (G) that was represented in 61% of the 28 bats examined from Grenada. This haplotype lineage is not unique to Grenada, but must be extremely rare elsewhere in the Antilles. Indeed, it was recovered from only one of 134 (0.7%) bats from Bequia and St. Vincent north through Jamaica. This single individual with a G haplotype was obtained on St. Vincent (1/20 bats examined). A third component of the genetic diversity on Grenada comes from the SV haplotype lineage, which was obtained from 10 individuals (36%). This mtDNA is typical of *A. j. schwartzi* on St. Vincent (Pumo et al., 1988) and also has been isolated from *Artibeus planirostris* collected in French Guiana (Pumo et al., 1996). Finally, it is noteworthy that the J haplotype lineage, which predominates in the Greater Antilles, is rare in *A. j. grenadensis* (Phillips et al., 1991), being found so far in a single individual (3.6%). The rarity of the J haplotype is consistent with the hypothesis that *Artibeus jamaicensis* on Grenada reached the island from the south rather than the north.

Comparing the means of measurements of male and female *A. jamaicensis* from Grenada (Table 1) using t-tests, we found that there were no secondary sexual differences in the eight measurements studied. The Jamaican fruit bat can potentially be confused with the other large species of *Artibeus* occurring on Grenada, *A. lituratus*, when attempting to identify the species under field conditions. However, the two species can be separated based solely using the measurement of the length of forearm. We have measured the length of forearm for 200 *A. jamaicensis* from the island, giving a mean of 58.0. The smallest individual, an adult male from along the Chemin River, had a forearm that measured 52.5, whereas the largest individual, an adult female from near Vendôme, measured 62.2. This can be compared with the range of length of forearm for 31 *A. lituratus*, which was 66.9 to 75.7.

Table 3 presents the reproductive data available for *Artibeus jamaicensis* from Grenada. Although these data are incomplete, only covering the period of March through August, they fit well with the data presented by Wilson et al. (1991) for populations of this species on Barro Colorado Island, Panamá. They concluded that the reproductive pattern of the Jamaican fruit bat is bimodal polyestry with females palpably pregnant in January and giving birth in late February and early March and again being palpably pregnant in April, May, or June with births in July and August. Although our data set is limited for the period of January through April, we have data for six females taken in early March (Table 3). One of these females was carrying a juvenile male with a total length of 58, two were noted as having near term fetuses, and three were noted as having small fetuses. Although not conclusive, these data would fit the pattern reported by Wilson et al. (1991). Our data are more complete for the period covering the second peak of reproductive activity and they do fit very nicely with the second peak of pregnancy in May-June with births in July-August as seen in Panama (Wilson et al., 1991). In addition to the data in Table 3, we took three flying subadults in a sample of 57 individual in late May. Lengths of forearms of 58.2, 58.7, and 59.0 indicated that these individuals had reached adult size even though some of the phalangeal epiphyses had not closed. In a sample 39 individuals taken on 11 August, 16 were considered to be juveniles or subadults with the length of forearm ranging from 39.1 to 59.1.

Table 3.—Reproductive data recorded for *Artibeus jamaicensis* from Grenada.

Date of Capture	Females				Males	
	Total no.	No. pregnant	Crown-rump length	No. lactating	No.	Length of testes
2 March	6	5	—	1	0	
23 May	3	3	15.7 (13-20)	0	2	5, 5
24 May	6	3	24.0 (10-33)	0	1	1
25 May	—				5	5.2 (2-7)
26 May	15	10	14.5 (6-22)	2	4	4.5 (4-6)
27 May	11	6	14.0 (6-20)	2	2	7, 7
28 May	7	4	17.3 (6-25)	1	5	5.9 (4-8)
29 May	5	3	11.0 (10-20)	0	0	
30 May	29	25	16.2 (5-40)	1	1	7
31 May	1	0		0	0	
1 June	1	1	23	0	0	
18 July	1	1	—	0	3	7.8 (7-9)
19 July	8	4	—	0	2	5, 7.5
16-17 August	15	0		2	2	5, 9

These data again are directly comparable to those reported by Wilson et al. (1991).

Artibeus lituratus palmarum

J. A. Allen and Chapman, 1897

Greater Fruit-eating Bat

Specimens examined (46).—ST. ANDREW: Birch Grove, 2 (UNSM); 0.4 km S, 0.4 km W St. Margaret, 1600 ft, 12°06' N, 61°41.5' W, 1 (CM). ST. DAVID: 1 1/4 km S, 3/4 km W Beaton, 12°01.5' N, 61°42' W, 4 (CM). ST. GEORGE: Chemin River, 1/2 km E Confer, 12°01' N, 61°43' W, 29 (23 CM, 6 UNSM); St. Paul's, 12°04' N, 61°44' W, 6 (CM); 1/2 km E Vendôme, 12°05' N, 61°42.5' W, 4 (2 CM, 2 TTU).

Additional record.—Douglaston (Jones, 1951).

Remarks.—The greater fruit-eating bat is widespread on Grenada, but we obtained large numbers of specimens only along the Chemin River. This species was taken at several sites along with its congener *A. jamaicensis*, which always was the more abundant of the two. The site along the Chemin River was near open sugarcane fields, but several large trees on both sides of the river formed a canopy in some areas. Away from the river vegetation was semitropical shrub forest and brush. At the time that we visited this area the river was nearly

stagnant, but formed several relatively large and deep pools. The report from Douglaston (Jones, 1951) was based on a single individual taken along with specimens of *A. jamaicensis* from the roof of a distillery.

We follow previous authors in assigning our specimens to the subspecies *palmarum* with a type locality at Port of Spain, Trinidad. Comparing the measurements of our specimens in Table 1 with those given by Dalquest (1951), Goodwin and Greenhall (1961), and Davis (1984) for specimens from Trinidad revealed mean values that were similar and had a broad overlap in the range of the measurements. T-tests of the eight measurements presented in Table 1 revealed no significant secondary sexual variation in our sample. As pointed out previously, it is not always easy to separate the greater fruit bat from the Jamaican fruit bat under field conditions. On Grenada, however, there is no overlap in the length of forearm of these two species. Thirty-one greater fruit bats had an average length of forearm of 70.4 with a range of 66.9 to 75.7, as compared with 52.5 to 62.2 for the Jamaican fruit bat. The smallest of the greater fruit bats was an adult female from near Vendôme and the largest was an adult female from St. Paul's.

Reproductive data for the greater fruit bat on Grenada are limited and does not allow discerning the pattern of reproduction. The reproductive cycle of this species is variable on the mainland (Wilson, 1979), with

a single young produced in northern Middle America and Mexico, in Costa Rica and Panama it has a bimodal cycle, and in Colombia the large fruit bats is a continuous breeder with bimodal activity peaks. Only one pregnant female was recorded in our sample from Grenada, which was taken on 29 May with an embryo with a crown-rump length of 7. Six non-pregnant females were noted on 23-24 May. Lactating females were taken on 23 and 29 May. The mean length of testes of 11 adult males captured between 23 May and 2 June was 5.6 (3-7).

Sturnira lilium serotinus
Genoways, 1998
Yellow-shouldered Bat

Specimens examined (7).—ST. ANDREW: Birch Grove, 3 (UNSM). ST. GEORGE: 1/2 km E Vendôme, 12°05' N, 61°42.5' W, 4 (CM).

Remarks.—These specimens constitute the first records for yellow-shouldered bats from Grenada. This species is known as far north in the Lesser Antilles as Dominica (Jones and Phillips, 1976) and a closely related species, *Sturnira thomasi*, is known from Guadeloupe (Genoways and Jones, 1975) and Montserrat (Pedersen et al., 1996). This material recently has been described as a new subspecies (Genoways, 1998) based upon its cranium being proportionally narrower than the population of *Sturnira lilium lilium* from Trinidad and overall smaller size (Table 1) than other Antillean forms of the species (*angeli*, *luciae*, *paulsoni*, and *zygomatus*; Jones and Phillips, 1976). Males were significantly (t-test) larger than females in greatest length of skull, condylobasal length, length of maxillary toothrow, and mastoid breadth (Table 1).

We collected three of our specimens in nets over a branch of the Balthazar River and an adjacent area behind the Police Station in Birch Grove. Vegetation in the area was a mixture of fruit and native trees. When we visited the site on 26 May 1987 the fruits on the mango, guava, and nutmeg trees were ripening and there was considerable activity by bats during the night. There was no canopy over the fairly broad river, which contains huge boulders with water braiding among them. The site at Vendôme where the other four specimens were captured is described in the account for *Noctilio*.

Females taken on 25 and 26 May were lactating, whereas a female taken on 30 May evinced no gross reproductive activity. Males taken on 25 and 26 May had testes that measured 6 and 3, respectively, in length.

Myotis nigricans nigricans
(Schinz, 1821)
Black Myotis

Specimens examined (3).—ST. DAVID: 1 1/4 km S, 3/4 km W Beaton, 12°01.5' N, 61°42' W, 1 (CM). PARISH UNKNOWN: no specific locality, 2 (NMNH).

Remarks.—Koopman (1968, 1994) assigned a specimen from Grenada to *M. n. nigricans* and we have maintained this arrangement here. LaVal (1973) in his revision of the Neotropical bats of the genus *Myotis* described a new species from Martinique and Barbados in the central Antilles and recognized a distinct species occurring on Dominica. It has subsequently been reported from Guadeloupe (Masson and Breuil (1992), but he did not examine or assign specimens from Grenada to a species. We have compared our specimens with the descriptions given by LaVal (1973) and believe that Koopman's initial identification was correct. Our specimen from near Beaton has a longer tibia (tibia to forearm ratio is 0.43) characteristic of *M. nigricans* rather than *M. dominicensis* (tibia/forearm 0.35). The specimens from Grenada are smaller than *M. martiniquensis* and closely match measurements given by LaVal (1973) for *M. nigricans* from Venezuela. They have dorsal pelage that is darker at the base than the tip, which is characteristic of *M. nigricans*, and lack a sagittal crest on the cranium, which usually is present in *M. martiniquensis*.

The specimen from Beaton was an adult male with testes length of 3 on 2 June 1986. Other specimens are males taken in March 1928 and on 25 August 1929, with the former taken by Dr. Paul Bartsch and the latter by Rev. Sebastian Gates.

Our specimen from near Beaton was netted over a small stream in an area that was just being slashed and burned to open it for agricultural purposes. A poorly developed gallery forest formed a canopy at intermittent points along the stream. Away from the stream vegetation was semi-deciduous, thorny bushes and small

trees. The area was so disturbed that several hundred active snakes were observed during the evening of netting.

Molossus molossus molossus
(Pallas, 1766)
Pallas' Mastiff Bat

Specimens examined (50).— ST. GEORGE: Chemin River, 1/2 km E Confer, 12°01' N, 61°43' W, 30 (28 CM, 2 UNSM); St. George's, 17 (MCZ); 1/2 km Vendôme, 12°05' N, 61°42.5' W, 2 (CM). PARISH UNKNOWN: no specific locality, 1 (NMNH).

Remarks.— This insectivorous species is far more abundant on Grenada than our collections would indicate. It easily is identified by its high rapid flight in the earliest evening, while swifts and other birds are still active. Pallas' mastiff bats are undoubtedly far more abundant currently on Grenada than prior to human habitation because man-made structures are now their primary roosting site. As pointed out by Allen (1911) this species "lives in colonies underneath the roofs of houses. Buildings covered with galvanized iron sheeting are especially favored by it since the small holes left open where the convexities of the sheeting meet the rafters afford ready ingress to spaces between ceiling

and roof. A large colony inhabited the roof of a cottage at St. George's, and here a small series was easily obtained by placing a dipnet over one of the openings. The owner of the house told us that the bats were active all night, constantly coming and going." This species also is captured easily in mist nets set over large calm pools of water with little or no canopy. These areas allow these bats to drink, while only slightly slowing their rapid flight.

The systematic relationships of the small mastiff bats occurring in the Antilles is still a matter of considerable debate (Miller, 1913b; Koopman, 1968; Dolan, 1989; Jones, 1989). Dolan (1989) made the most thorough analysis of the complex nomenclatural history and relationships of these small bats and we follow her arrangement and that of Koopman (1994) in assigning populations on Grenada to the nominate subspecies. Our specimens are clearly larger (Table 1) than specimens from southern Mexico, Guatemala, and El Salvador reported by Dolan (1989), but a detailed analysis of variation throughout the range of species will be necessary before a final decision will be possible on allocating all specimens to the appropriate taxon.

Of 10 females examined for reproductive activity on 23 May 1980, nine were pregnant. Embryos ranged in crown-rump length from 12 to 16.5, with a mean of 13.2.

DISCUSSION

Grenada, being situated at the southern end of the Lesser Antilles, occupies an interesting zoogeographic position. It is positioned to receive bat species invading the Antilles from the south via Trinidad or Tobago and the South American mainland and for Antillean endemic species to arrive from the north via St. Vincent and the Grenadines. We do believe that all of the species of bats currently on islands in the Caribbean region have arrived via over water migration (Baker and Genoways, 1978; Pregill, 1981; Morgan and Woods, 1986; Pumo et al., 1988, 1996; Phillips et al., 1989, 1991) rather than being the result of vicariance (Rosen, 1975). All species of bats on Grenada can be classified as either recent invaders from the south or as widespread species for which no dispersal route is discernible (Koopman, 1968, 1989; Jones and Phillips, 1970; Baker and Genoways, 1978; Jones, 1989).

The origin of the chiropteran fauna of Grenada stands in contrast to the other group of volant vertebrates—birds. The avifauna of Tobago is composed of 70 species of which 50 are of probable South American origin and 20 are widespread species, whereas the avifauna of Grenada consists of 35 species of which 9 are of Antillean origin, 6 of South American origin, and 20 are widespread species (Lack 1976). Lack (1976) was so struck by the faunal differences between these two islands that he proposed "Bond's Line" as the faunal boundary between the West Indian fauna of Grenada and the South American fauna of Tobago. There has been a plethora of recent investigations of mammalian fauna of the West Indies, especially of bats, to the point that we believe that the zoogeographic boundary of the West Indian subregion can now be defined with relative certainty. We here propose to call this boundary demarking the

West Indian Faunal subregion as "Koopman's Line" in honor of our late colleague Dr. Karl F. Koopman, who published many of these studies, including the first delimiting the boundaries of the West Indian subregion (Fig. 1).

Our West Indian Faunal subregion of the Neotropical region differs from the one presented by Hershkovitz (1958) in several details. We are excluding Grenada and the Grenadines from the region. We have questioned the placement of the Grenadines because the bat fauna of this series of islands is poorly known. The four species reported from this complex of islands (Jones, 1989) are all widespread in distribution and give no indication of their faunistic relationships. We anticipate that one or two (*Monophyllus plethodon* and/or *Brachyphylla cavernarum*) of the Antillean endemics known from St. Vincent probably also occur at least on Bequia, which is just over 2 km south of St. Vincent and can be seen from there. This means that Koopman's Line may eventually be found to bisect the Grenadines.

Along the south side of the subregion we are excluding Trinidad, Tobago, Margarita, Aruba, Bonaire, and Curaçao (Koopman, 1958, 1959; Husson, 1961; Goodwin and Greenhall, 1961; Smith and Genoways, 1974; Genoways and Williams, 1979; Carter et al., 1981; Eshelman and Morgan, 1985; Morgan and Woods, 1986). In the west we exclude Isla Cozumel, Isla Mujeres, Halfmoon Cay, Roatan, Bonacca, and San Andreas (Koopman, 1959; Jones et al., 1973). We differ from Koopman (1959) in excluding San Andreas, which he included because of its proximity to Providencia; however, the only species currently known from San Andreas is *Artibeus jamaicensis*, but this species is widely distributed so its mere presence does not provide much insight into zoogeographic patterns. We do agree with Koopman (1959) in including Providencia in the West Indian subregion because of the presence of Antillean endemic *Natalus brevimanus* in addition to *A. jamaicensis*. We also include the Swan Islands in the West Indian subregion because of the occurrence of the endemic hutia (*Geocapromys thoracatus*), which is of Antillean affinity (Koopman, 1959; Morgan, 1985). In the north we include all of the Bahamas (Koopman et al., 1957; Baker and Genoways, 1976; Buden, 1986; Morgan and Woods, 1986; Jones, 1989).

Currently, the relationship of south Florida and the Florida Keys to the West Indian Faunal subregion is open to question because the bat fauna is poorly known and bats seem to be relatively rare in the area; however, there is a growing body of data that would seem to relate this area to the subregion. Recently, Frank (1997) reported *Molossus molossus tropidorhynchus*, the Cuban subspecies of this bat, from four of the Keys, including Key West, Vaca Key, Boca Chica Key, and Stock Island. He found three established colonies, but could not be certain whether their origin involved over water dispersal from Cuba (Silva Taboada, 1979) or human transportation. Fossil and Recent specimens of *Eumops glaucinus floridanus* document that this Neotropical species has been in Florida since the Late Pleistocene (Koopman, 1971; Morgan, 1991). Although the nearest population of this species is on Cuba (Silva Taboada, 1979), Morgan (1991) could not rule out that this species had dispersed into Florida via the Gulf Coast from mainland populations of the species in Mexico. There are at least two reports of *Artibeus jamaicensis* from Key West (Maynard, 1872; Lazell and Koopman, 1985), but because the specimen was not preserved in either case, these reports can not be verified. Further doubt was cast by Humphrey and Brown (1986) who disputed the identification of the photographed bat in Lazell and Koopman (1985). Morgan (1991) acknowledged that *A. jamaicensis* could occur on Key West, but concluded that they were only accidental occurrences and that no population had been established. Fossils of two Neotropical bats lend some additional evidence to the West Indian relationships of south Florida and the Florida Keys. The modern species *Mormoops megalophylla* only is known as a fossil from Florida, Bahamas, Dominican Republic, Cuba, and Jamaica. Morgan (1991) concluded that the Florida and West Indian specimens were "virtually identical in size" and, furthermore, these specimens could not be distinguished from modern mainland populations of the species from Mexico and South America. Morgan (1991) also reported a fossil bat from Florida as *Pteronotus* cf. *P. pristinus*, which is a fossil species described by Silva Taboada (1974) from Cuba. Although the evidence is not compelling enough to include south Florida and the Florida Keys in the West Indian Faunal subregion without question, the evidence does seem to be accumulating and we should certainly be aware that this relationship may exist.

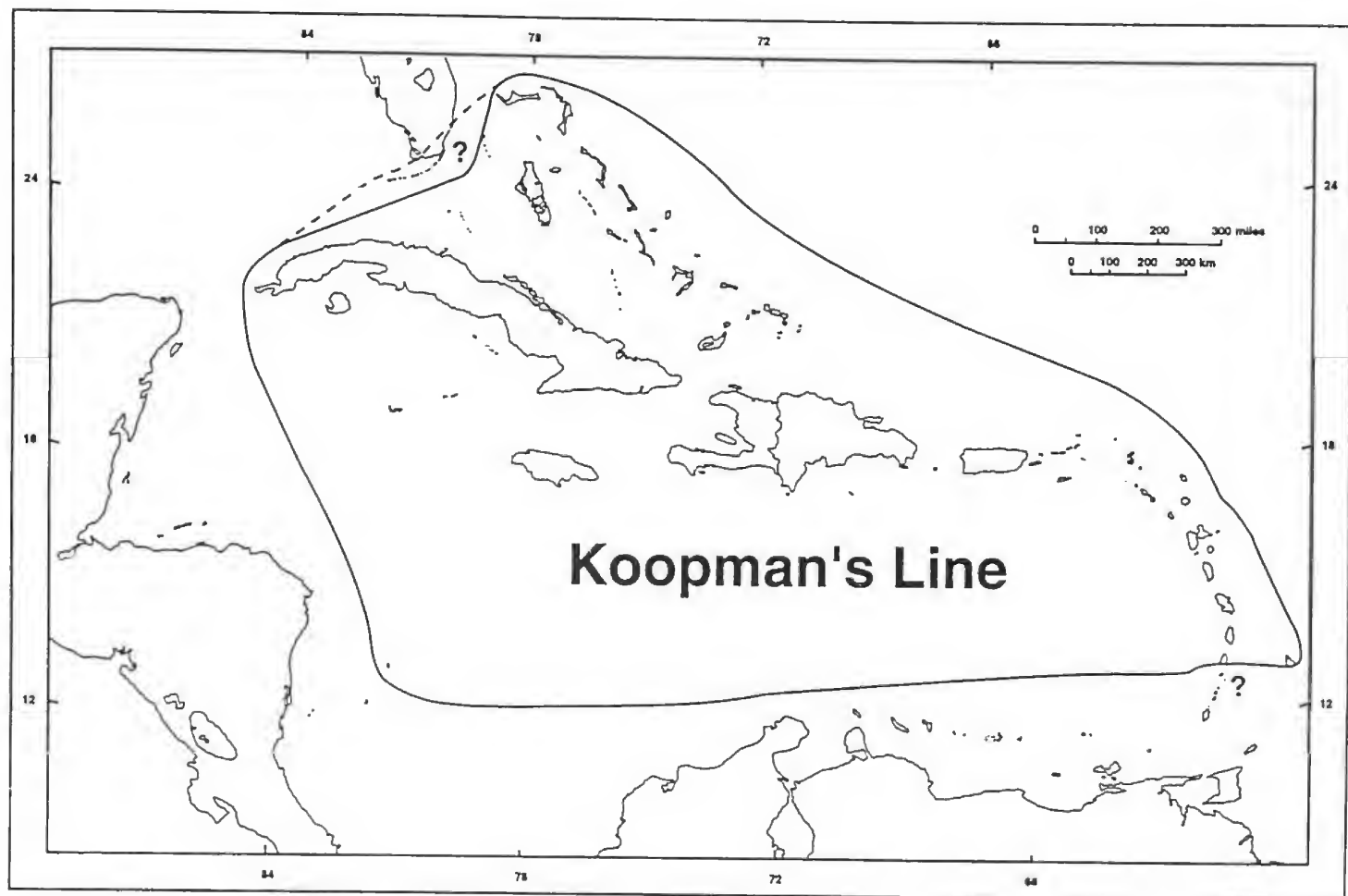


Figure 1. A map of the Caribbean region showing the limits of Koopman's Line, which defines the boundary of the West Indian Faunal subregion based upon mammalian distribution patterns.

Like the avifauna data, our data reflect a disparity in the size of the chiropteran fauna between Tobago and Grenada (Lack, 1976; Wunderle, 1985). Twelve species of bats are known from Grenada, 20 species are known from Tobago (Eshelman and Morgan, 1985), and 64 species are known from Trinidad (Carter et al., 1981). In the avifauna, 35 species have been recorded from Grenada and 70 from Tobago. The chiropteran fauna does not quite reach a doubling of the number of species on Tobago compared to Grenada that the avifauna does, but it is 1.66 times larger. The difference in the size of the fauna between Trinidad and Grenada is consistent with island biogeographic theory, which predicts that island size and distance to the source area (mainland) are important factors. Tobago on the other hand is quite similar to Grenada in size (300 sq km versus 311 sq km, respectively), elevation (580 m versus 840 m), distance from South American mainland (both about 130 km, although Tobago is only about 35 to 40 km from Trinidad), climate, cultivated crops, and area under cultivation

(Wunderle, 1985). Previous authors (Eshelman and Morgan, 1985; Wunderle, 1985) have not found an explanation for this phenomenon. It can not be attributed to the size of the islands, which Morgan and Woods (1986) found to account for 69% of the mammalian species diversity on Antillean islands. They believed that the other 31% could be related to "variables such as habitat diversity and distance from source areas." Habitat diversity can not explain differences because in the Antilles habitat diversity is directly affected by elevation, which in this case would favor higher diversity on Grenada. We believe that the most important factor affecting the mammalian species diversity of Tobago and Grenada is distance from the source area, which in the case of Tobago is primarily Trinidad, whereas the source for the fauna on Grenada is either Trinidad or the South American mainland, or both. This makes the source for Grenada at least three times further away than for Tobago.

McFarlane (1989) examined patterns of co-occurrence of species in the Antillean bat fauna and concluded that... "The structure of bat assemblages on the Greater Antilles is dominated by the co-occurrence of single island endemics, whereas a similar structure in the Lesser Antilles is dominated by the co-occurrence of undifferentiated South American taxa." We believe that the situation in the southern Lesser Antilles is more complex than this conclusion would indicate. If the co-occurrence of bat species southward from Montserrat to Grenada is considered, the species *Noctilio leporinus*, *Artibeus jamaicensis*, and *Molossus molossus* are found to occur on all nine of these islands or island groups. This would support the conclusions of McFarlane (1989) because these are widespread species. On the other hand, if Grenada and the Grenadines are eliminated from this group of islands as being outside of the West Indian subregion, *Monophyllus plethodon* and *Brachyphylla cavernarum* will be added to the list of co-occurring species of bats on these islands. Additionally, *Ardops nichollsi* occurs on all except Barbados. These are three endemic Antillean genera with *B. cavernarum* and *M. plethodon* being known from Puerto Rico east and south in the Lesser Antilles and *A. nichollsi* being endemic to the Lesser Antilles. This gives a different looking assemblage of co-occurring species that is balanced between Antillean endemics and widespread species, which is in contrast with the conclusion of McFarlane (1989).

Traditionally, zoogeographic analyses of Antillean bats have been based on two types of data: (1) presence or absence of a particular species on an island; and (2) presence or absence of phenotypic differences between animals on one island and those on other islands or mainland. Plotted geographically, such information has been and continues to be informative. Technology now is available to begin to test some of the resulting hypotheses about historical gene flow and genetic diversity. In the account of the Jamaican fruit bat, *Artibeus jamaicensis*, we summarized some of the mtDNA haplotype data that implied the Grenada population had at least three genetic influences (north, south, and northeastern coastal South America; Pumo et al., 1996). To explore this further, we returned to our original data set (see Phillips et al., 1989, 1991) consisting of mtDNA RFLPs (restriction fragment length polymorphism) from 162 specimens obtained on Jamaica, Puerto Rico, Anguilla, St. Lucia, St. Vincent, Bequia, Barbados, and Grenada. For additional compari-

son we also included 12 specimens from the Yucatan Peninsula. We scored each animal based on our previous work and used previously unavailable analytical software (Arlequin, ver 1.0, Schneider et al., 1996; Holsinger and Mason-Gamer, 1996) to estimate nucleotide diversity per island and genetic distances among islands in pairwise comparisons. The complete analysis goes beyond the present paper and will be presented elsewhere (Phillips et al., in preparation), but the data strongly support our idea that Grenada falls outside the West Indian faunal subregion. Indeed, genetic distance (F_{ST}) values between Grenada and the other seven islands were 0.435 (St. Vincent), 0.446 (Bequia), 0.450 (St. Lucia), 0.92 (Barbados), 0.509 (Anguilla), 0.578 (Jamaica), and 0.609 (Puerto Rico), and all comparisons were highly significant ($P < 0.01$). By way of comparison, the F_{ST} value between Puerto Rico and Anguilla and Anguilla and Barbados was 0.009 and was nonsignificant. The striking nature of the data is further illustrated by the fact that although the F_{ST} value (0.362) between Grenada and the Yucatan Peninsula is significant ($P < 0.01$), it is far lower than those between Grenada and other Antillean islands.

The foregoing illustrates that gene flow (historical or contemporary) is not necessarily uniform in geographically widespread species with apparently strong dispersal power. The significant genetic distance between *A. jamaicensis* on Grenada and conspecifics to the north is consistent with the overall distributional pattern of Antillean bat species. The open question remains: is there some barrier to gene flow between Grenada and islands to the north, or is the genetic distance and faunal composition a reflection of "recent" post-Pleistocene invasion of Grenada by species that have not yet progressed northward? In a previous analysis (Phillips et al., 1989) we hypothesized that the Grenadines were more of a "filter" than a stepping-stone pathway to the north. Our suggestion was based on the fact that these are small, extremely arid, islands with limited nutrient resources. Indeed, some (e.g., Mustique) have natively thorny vegetation and completely lack standing fresh water. For fruit bats, the only food is probably provided by cultivated plants. We imagined that such islands effectively could become "sinks." Although our mtDNA data from *A. jamaicensis* do not speak to the question of timing, the significant genetic distance between Grenada and islands to the north and northeast (Barbados) is consistent with metapopulation theory and "source-sink" dynamics (for

example, Gaggiotti, 1996). The analysis also strongly supports our concept of “Koopman’s Line” and the West Indies Faunal subregion.

In conclusion, it is important to note our observations on the status of bat populations on Grenada. Although some of the species are rare on Grenada, for example, *Pteronotus davyi*, *Micronycteris megalotis*, *Artibeus glaucus*, and *Sturnira lilium*, we believe that this is a natural phenomenon characteristic of island populations. We believe that these species and others on Grenada will continue to survive as long as current eco-

logical situation prevails. Montane habitats must be preserved and the current forest reserves are accomplishing this goal. Representation of low scrub habitat must be preserved as well. Although this habitat currently is well represented on the island, it probably is the most heavily impacted by humans and its continued health must be monitored. Other areas that should be monitored into the future are lowland caves and shelters used by several species as roosting sites. These sites must be preserved and not disturbed if many of the bat species on Grenada are to maintain their current status.

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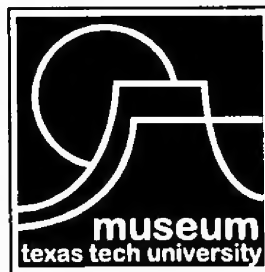
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It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

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